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Population Viability of Mega-Herbivores in Manyara Ranch, Tanzania, in a Climate Change Context

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Abstract

Declines in wildlife populations represent a serious environmental threat. One cause of declines has been climate change, which has led to increased aridity and droughts in some systems, such as the savannah ecosystems of sub-Saharan Africa. Climate change is expected to result in more frequent and intense droughts and the effects on wildlife populations are largely unknown. I examined impacts of droughts on wildlife in Manyara Ranch, a community-run conservation area in Tanzania, by assessing population trends of herbivores collected over the past decade and modeling the viability of these populations into the future under different scenarios of drought periodicity and intensity. Densities of nine herbivore species were estimated on a yearly basis from 2003 to 2014. These densities were then used to create species-specific PVAs, including models examining the impacts of various periodicities (5-, 10-, and 20-year increments) and intensities (population reductions of 10%, 20%, and 30%). Baseline population persistence varied between species from 0% to 100%, while sensitivity models trended towards most species showing significantly lower persistence percentages for more frequent and intense droughts, particularly with high intensity droughts every five years. Elephants demonstrated the lowest persistence with or without droughts, while Grant's gazelle had the highest persistence throughout all models. Continued monitoring of populations is a necessity, and increased actions should be taken to preserve populations of priority species, including protecting migratory routes and limiting poaching.

Keywords: population viability analysis; climate change; distance sampling; Tarangire-Manyara Ecosystem; wildlife density; herbivores

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Tanzania

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Vermont

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Introduction

Monitoring and predicting wildlife population changes have become increasingly important management tools for species, especially those on the decline. The World Wildlife Fund estimated that vertebrate populations worldwide declined by approximately 50% between 1970 and 2010 (World Wildlife Fund, 2014). This trend is noticeable throughout Africa, where populations of several large species have been decreasing. It has been estimated that since the 1970s, the abundance of African large mammals in protected areas has been halved, especially in the biologically rich area of East Africa (Craigie et al., 2010). In major ecosystems including Maasai Mara in Kenya and Tarangire-Manyara in Tanzania, ungulate species such as Cape buffalo (*Syncerus caffer*), giraffe (*Giraffa camelpardalis*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*), eland (*Taurotragus oryx*), lesser kudu (*Tragelaphus imberbis*), and warthog (*Phacochoerus africanus*) have all experienced declines since the 1980s (Ogutu et al., 2009; Stoner et al., 2006). Notably in the Tarangire-Manyara Ecosystem, the population of wildebeest (*Connochaetes taurinus*) declined by 88% during the 2000s (Tanzania Wildlife Research Institute, 2001). Declines have been mainly due to impacts on ungulate migration routes, which often lack sufficient protection (Western et al., 2009). Reasons for declines include hunting and habitat loss (Bolger et al., 2008; Caro et al., 1998*b*). However, another major factor determining the maximum herbivore biomass within an area is the amount of rainfall an area receives (Coe et al., 1976); as climate change creates more variable rainfall patterns, wildlife populations have the potential to be further impacted.

Due to already existing climatic variability throughout Africa, tracking the long-term changes in weather patterns can be somewhat difficult. Oscillations in rainfall can in some areas follow an 18-year cycle, although in others the variation can be as little as 2-3 years (Mason and Jury, 1997). The climate of the sub-Sahara is dictated by the North Atlantic Oscillation (NOA) and the El Niño Southern Oscillation (ENSO), which are also impacting growing desertification and vegetation productivity (Oba et al., 2001). While the NOA and ENSO do account for some of the variation seen, it has been noted that

there has been a consistent decrease in rainfall during the dry season since the 1980s (Ogutu and Owen-Smith, 2003).

Decreases in wildlife populations appear to be directly correlated with decreases in precipitation. In Kruger National Park in South Africa, species such as greater kudu (*Tragelaphus strepsiceros*), waterbuck, and eland have experienced large declines, likely due to the changing rainfall patterns, although other species such as zebra, wildebeest, giraffe, and impala appear better able to manage (Ogutu and Owen-Smith, 2003). Similar trends were found in Kenya, although notably elephants (*Loxodonta africana*) were inclined to migrate out of a region during times of drought (Augustine, 2010). Even with some species likely being able to manage increased droughts, substantial declines in biodiversity are expected, with the potential for 10-15% of mammal species in Africa to be either critically endangered or extinct by 2050 and 25-40% critically endangered or extinct by 2080 (Thuiller et al., 2006).

In the face of declines and climate change, setting aside land for protection represents an important management approach. Tanzania currently has multiple types of protected areas, with national parks being the most protected, prohibiting settlements and all forms of resource extraction; game reserves allow limited hunting but are otherwise similar to national parks, while game-controlled areas allow for extraction and settlement but still limit hunting (Caro et al., 1998*a*). Wildlife-management areas are a recent development, which are locally managed and usually form buffer zones around national parks, with the goal of promoting large mammal conservation and local community involvement in conservation (Caro et al., 2009). Additionally, many communities have begun independently setting aside land for wildlife habitat. Conservation is most effective when human activity is absent or limited and where enforcement occurs on-site, which has been seen to maintain high ungulate densities (Caro et al., 1998*a*).

Understanding the impacts of setting land aside for protection incorporates multiple facets. While widespread population declines have occurred in protected areas, this is not an indication of the failure of protected areas, as there is no comparison to what would be occurring without the protected areas, and conditions outside of protected areas are likely still having a strong impact on the conditions within them (Craigie et al., 2010). One method of combating this degradation outside of parks can be seen in the

development of community protected areas (Caro et al., 2009). By creating an economic incentive for local communities to manage wildlife populations, it is hoped that wildlife conservation can then be considered a viable form of land use (Sachedina, 2006).

Traditionally, the effectiveness of protected areas has been measured by the amount one retains the integrity of its environment in comparison to the surrounding lands; however, this method has not been found to be effective in grasslands and similar habitats, and thus population monitoring over time is a more viable tool (Craigie et al., 2010). This is particularly important in East Africa, where ungulate species tend to leave protected areas for seasonal migrations (Morrison and Bolger, 2012). Wildebeest migration in the Serengeti-Mara Ecosystem includes areas of limited protection that are threatened by poaching and agriculture; as a result, wildlife-management areas are an important aspect of conservation due to their status as buffer zones (Thirgood et al., 2004). Community-oriented conservation areas are a new concept in wildlife protection, and studies continue as to whether this is an effective approach to conservation.

Population viability analysis (PVA) is a means of predicting population trends of a species over a set period, particularly in terms of persistence or extinction. Creating a predictive model requires existent data on the dynamics or demographics of the subject population (Boyce, 1992). Parameters and viability criteria can vary between PVAs, as they are often dependent on the ecology of the subject species, but most PVAs incorporate some form of stochastic model to predict extinction probabilities (Beissinger and Westphal, 1998). While PVA estimates should not be considered absolute predictors for wildlife populations, predicted outcomes for PVAs closely match observed outcomes, making them a valuable management tool (Brook et al., 2000).

I examined the population viability of nine mega-herbivore species in a community-run conservation area, Manyara Ranch in Tanzania, with the objectives of assessing the potential impacts of increased droughts and of highlighting the species of greatest conservation concern. I used data collected over a 10-year period to estimate population characteristics, then conducted a PVA on each species and assessed viability over a 100-year time frame. For each analysis, I also simulated the impacts of droughts of varying periodicity and intensity on the viability of each species. Resident species were expected to fare better than migratory species, and water-independent species were

expected to fare better than water-dependent species. The results provide an assessment of the potential impacts of climate change on mega-herbivores that will help inform decision-making at Manyara Ranch and other conservation areas in Tanzania.

Methods

Study Area

Manyara Ranch (MR) is a community-run conservation area in the Tarangire-Manyara Ecosystem of northern Tanzania (3º23'S, 35º35'E). The ranch covers approximately 182 km^2 and lies within the dispersal corridor between Lake Manyara National Park (LMNP) and Tarangire National Park (TNP). Management of MR allows for controlled cattle-grazing within the boundaries but does patrol to prevent bush meat poaching. Pairing community with conservation is one focus of MR, which provides corridor habitat while also helping support the local community: funds raised by MR go back to support community projects, and, despite the potential impacts that cattle grazing can place on wildlife, allowing such land application gives the community incentive to continue investing in conservation. The Manyara Trust Lands Conservation Area (of which MR is part of) "was established and exists as part of protected area networks in Tanzania"; additionally, they are looking "to conserve the MTLCA as part of the Tarangire-Manyara ecosystem for biodiversity, tourism and socio-economy of MTLCA and adjacent areas" (Tanzania Land Conservation Trust, 2011).

The ecology of the Tarangire-Manyara Ecosystem (TME) is dictated by rainfall, which is bimodal with peaks in precipitation in March-May (long rains) and November-December (short rains) (Mwalyosi, 1981); the period of June-October is generally referred to as the dry season. Additionally, annual rainfall can vary substantially from year to year. For example, rainfall was over three times greater in 1968 than it was in 1969 (1500 mm to 480 mm) (Mwalyosi, 1981). Wildlife behavioral responses to times of low rainfall can vary between moving to different areas (as seen in but not limited to elephant, eland, zebra, and giraffe) or switching between grazing in the wet season and browsing in the dry season (as seen in impala) (Augustine, 2010); thus, not all local

population changes during dry periods are due to mortality and may be a result of migration.

The two main habitat types in the TME are poorly-drained grasslands and *Acacia* woodlands (Prins, 1987). This dichotomy provides habitat for a variety of herbivores, including both grazers and browsers. Land use has increasingly been shifting towards agriculture outside of protected areas, which has led to serious degradation of the soil (Prins, 1987). The entire TME has a human population of approximately 350,000 and a cattle population of 1,000,000, with a majority of people following a pastoralist lifestyle (Tanzania Land Conservation Trust, 2011).

Dominant large wildlife species in the ecosystem include elephant, Cape buffalo, zebra (*Equus burchelli*), wildebeest, and eland, with other present species including lesser kudu, giraffe, warthog, impala, waterbuck, and Kirk's dikdik (*Madoqua kirkii*) (Tanzania Land Conservation Trust, 2011). Wildebeest are grazers notable for their synchronicity in birthing—80-90% of all calves are born within a three week period at the beginning of the long rains (Estes, 2012). While other species tend to reproduce during the long rains, none do so with the same coordination as wildebeest. Elephants are reliant on sufficient quantities of water (Estes, 2012). The presence of elephants is also of great importance for their ability to destroy trees. Elephants have been credited with the decline of woodland in certain areas (Western and Maitumo, 2004). Monitoring elephant populations is critical for not only determining whether the population is too low but also for estimating if there is a local surplus, exceeding the carrying capacity.

Data Collection

Manyara Ranch collected population data on local wildlife from 2003 to 2008 and School for Field Studies (SFS) researchers collected data from 2011 to 2014. In both cases distance sampling along transects was used to estimate population sizes (Thomas et al., 2009), and the main difference in methodology was in the number and length of transects between data collection periods. Old data were collected with fewer, longer transects, while recent data collection employed more transects of shorter lengths (Table 1). Data were collected through vehicle transects in MR. For data from 2011 to 2014, each transect was 2 km long, with 500 m between each transect. Transect length was measured using the vehicle odometer. Time and GPS coordinates were recorded for both

the start and end of each transect. Most transects followed roads within MR, but some encompassed off-road driving for more comprehensive coverage of the study area. Each vehicle contained three spotters in addition to the driver and a local guide.

Table 1. Effort for line distance of surveys conducted in Manyara Ranch, 2003-2014. Bold indicate surveys used to estimate model parameters.

Survey	# of transects	Line length (km)	Surveyors
2003, long rains	**4**	**297.2**	**MR**
2004, dry	4	369.7	MR
2004, short rains	4	245.7	MR
2005, long rains	**4**	**209.1**	**MR**
2007, dry	4	299.1	MR
2007, short rains	3	174.18	MR
2008, long rains	**4**	**101.5**	**MR**
2008, short rains	4	283.7	MR
2011, short rains	45	129.47	SFS
2012, long rains	**41**	**174.0**	**SFS**
2012, dry	41	81.3	SFS
2012, short rains	37	198.53	SFS
2013, long rains	**36**	**70.6**	**SFS**
2013, dry	34	66.4	SFS
2013, short rains	46	88.4	SFS
2014, long rains	**39**	**73.4**	**SFS**
Total	350	2862.28	—

Along each transect, researchers recorded information for all mammal species of mongoose-size or larger (including any humans and domesticated animals) and for ostriches (*Struthio camelus*). Most species were noted for use in long-term monitoring but were not included in the analysis of this project. One group of the same species was considered a single observation, with individuals separated by at least 50 m with no other individuals in between being considered in separate groups. For each observation, GPS coordinates were taken, and the perpendicular distance of the observation to the road was

measured with a rangefinder. The count of total individuals in each observation was also recorded.

Population Analysis

Data from 2003-2008 were initially analyzed separately from the 2011-2014 data due to the differing collection methods. The software program Distance 6.0 was used for estimating population densities, which relies on the assumptions that 1) all animals at a distance of 0 m are seen, 2) animals do not move prior to detection, and 3) measurements are exact (Thomas et al., 2009). Assumption 3 was met through the use of a rangefinder, while Assumption 2 was enforced by measuring to the initial location of the wildlife when it was spotted rather than where it may have moved to. Distance develops models based on the frequency of sightings versus the distance of sightings, which estimates effective transect width. From this, Distance can then provide density estimates for the entire study area through the application of various models. Densities of nine species were calculated, which were selected due to their prominence in the ecosystem: Kirk's dikdik, eland, elephant, giraffe, Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsonii*), impala, wildebeest, and Burchell's zebra. For each species and time increment, six models were fit for analysis. Four CDS analyses were run (uniform, half-normal, hazard-rate, and negative exponential); additionally, two MCDS analyses were run (half-normal and hazard rate), with season as the covariate to account for the variability of visibility due to vegetation growth (Thomas et al., 2009). Each species and time increment then had one model selected as the best fit, with the corresponding density estimate being used for further modeling. (Table 2). The best fit was selected based on the lowest AIC value and on visual fit, thus estimating species- and season-specific densities. While not all models had optimal chi-square goodness of fit probability, selected models had preferable probabilities over other models.

Table 2. Characteristics of detection functions used for calculating species density in Manyara Ranch, 2003-2014. CI is confidence interval, X^2 GOF-p is the chi-square goodness of fit probability.

Species	Detection probability, P_a	P_a 95% CI	Estimated strip width (m)	Model	X^2 GOF-p
Dikdik					
2003-2008	0.46	0.40-0.54	23.0	MCDS half-normal	
2011-2014	0.57	0.50-0.66	46.0	MCDS hazard-rate	
Elephant					
2003-2008	0.17	0.11-0.28	138.0	CDS hazard-rate	0.0753
2011-2014	0.59	0.47-0.75	297.6	CDS uniform	0.109
Eland					
2003-2008	0.45	0.00-1.00	135.6	MCDS half-normal	
2011-2014	1.00		500.0	CDS uniform	0.447
Giraffe					
2003-2008	0.19	0.17-0.21	149.2	MCDS hazard-rate	
2011-2014	0.64	0.58-0.70	320.1	MCDS hazard-rate	
Grant's gazelle					
2003-2008	0.26	0.20-0.33	77.5	CDS negative exp	3.99E-06
2011-2014	0.45	0.39-0.53	218.3	MCDS half-normal	
Thomson's gazelle					
2003-2008	0.56	0.47-0.66	112.1	CDS uniform	0.253
2011-2014	0.60	0.53-0.67	218.8	MCDS half-normal	
Impala					
2003-2008	0.33	0.29-0.38	66.3	CDS uniform	0.000
2011-2014	0.51	0.45-0.57	151.5	MCDS half-normal	
Wildebeest					
2003-2008	0.17	0.12-0.23	134.4	CDS hazard-rate	0.0162
2011-2014	0.71	0.65-0.77	282.3	MCDS half-normal	
Zebra					
2003-2008	0.23	0.21-0.25	91.4	CDS uniform	0.000
2011-2014	0.63	0.59-0.67	242.8	MCDS hazard-rate	

Population Viability Analysis

Population models were developed to estimate the viability of each species over a 100-year time period. Data were utilized from the long rains season each year. Years with missing data (2004, 2006-2007, 2009-2011) were estimated by either averaging the two surrounding years, or, in the cases where more than one consecutive year was missing, by assuming that each year the population changed by an equal number of individuals and filling in accordingly. Lambda values (N_{t+1}/N_t) were then calculated for each year of the

study period to determine the yearly growth rates, and an average lambda and standard deviation were estimated for each species. The study period spanned 2003 to 2014, except for wildebeest, which began in 2005; the 2003 count was significantly lower than any other count, and was thus omitted as an outlier.

For each year of the model, a random lambda value was drawn from a distribution determined by the standard deviation around the mean. This value was multiplied with the current population to provide a population for the following year. Each year of the model had a new value of lambda randomly drawn, which thus incorporated the stochasticy of the population.

Due to the open and migratory nature of the populations, the standard deviations of lambda tended to be quite broad, which resulted in two problems. The first was that the simulation often selected a negative lambda, which is not realistic. To prevent negative lambdas in the model, a function was included so that any time a negative lambda was supplied, the simulation would instead utilize the average lambda across all years. The second problem was that when populations did not reach extinction, most species tended to rise to unreasonable and unrealistic numbers. To prevent unrealistically high population estimates, a carrying capacity was introduced to the simulation. As no definitive carrying capacities existed for MR, a literature review of known species densities in various locations was conducted (Table 3). These densities were then used to estimate potential long rains densities reasonable to MR, which were approximated into carrying capacities (Table 4). The exact densities selected for use as the means for calculating a carrying capacity in MR were medians of existing data, but the range of data selected for estimating carrying capacity was informed by expert opinion on the study area. Additionally, densities erred on the side of being higher, particularly in regards to non-resident species, in order to account for the open nature of the populations. Carrying capacities were merely used as an upper boundary for populations and should not be considered hard estimates; wide variations in potential carrying capacities within a single species tended to have minimal impact on survivability but were necessary as there was a notable discrepancy between survivability with a carrying capacity and survivability without one.

Table 3. Literature review of species densities.

Species	Area	Density (animals/km^2)	Source
Dikdik	Tarangire Game Reserve, Tanzania	0.27-3.2	Lamprey, 1964
	Tsavo West NP, Kenya	15-25	Hofmann, 1973
	Arusha NP, Tanzania	53.1-68.3	Amubode & Boshe, 1990
	Serengeti NP, Tanzania	5-33	Estes, 1991
	Tsavo East NP, Kenya	107-112	Komers and Brotherton, 1997
	Mpala Research Centre, Kenya	138.7	Augustine, 2010
	Northern Tanzania	3-60	Foley et al., 2014
Elephant	North Bunyoro, Uganda	2.94-3.5	Laws & Parker, 1968
	Murichison Falls NP, Uganda	3.6	Laws, 1981
	Katavi NP, Tanzania	1.96	Caro, 1999
	Katavi NP, Tanzania	0.266	Caro, 2008
	Katavi NP, Tanzania	0.95	Waltert et al., 2008
	Hwange NP, Zimbabwe	1.26-4.67	Chamaillé-Jammes et al., 2009
	Kibale NP, Uganda	0.5	Wanyama et al., 2009
	Mpala Research Centre, Kenya	1.7	Augustine, 2010
	Tarangire Game Reserve, Tanzania	0.88	Foley et al., 2014
Eland	Katavi NP, Tanzania	1.45	Caro, 1999
	Lake Mburo NP, Uganda	4.1	Rannestad et al., 2006
	Katavi NP, Tanzania	0.359	Caro, 2008
	Continent average	0.39	Pettorelli et al., 2009
	Katavi NP, Tanzania	0.32	Waltert et al., 2009
	Mpala Research Centre, Kenya	0.37	Augustine, 2010
Giraffe	Nairobi NP, Kenya	0.72	Foster, 1966
	Timbavati Game Reserve, South Africa	5.3	Dagg and Foster, 1982
	Wankie NP, Zimbabwe	14.1	Dagg and Foster, 1982
	Katavi NP, Tanzania	2.17	Caro, 1999
	Katavi NP, Tanzania	0.98	Waltert et al., 2008
	Mpala Research Centre, Kenya	0.33	Augustine, 2010
Grant's gazelle	Ngorongoro Crater, Tanzania	5.5	Turner and Watson, 1964
	Ngorongoro Crater, Tanzania	4.8	Estes, 1967
	Narok rangelands, Kenya	2.8	Stelfox et al., 1986
	Mkomazi NP, Tanzania	0.14	Foley et al., 2014
Thomson's gazelle	Ngorongoro Crater, Tanzania	11.3	Estes, 1967
	Serengeti NP, Tanzania	78	Fryxell et al., 2005
	Simanjiro Plains, Tanzania	2.45	Rija and Hassan, 2011
Impala	Nairobi NP, Kenya	15-18	Leuthold, 1970
	Serengeti NP, Tanzania	19-32	Jarman, 1979
	Mkuzi Game Reserve, South Africa	80	Vincent, 1979
	Sengwa Research Area,	50-68	Murray, 1982

	Zimbabwe		
	Katavi NP, Tanzania	3.72	Caro, 1999
	Katavi NP, Tanzania	2.69	Caro, 2008
	Katavi NP, Tanzania	5.02	Waltert et al., 2008
	Mpala Research Centre, Kenya	20.3	Augustine, 2010
	Simanjiro Plains, Tanzania	7.95	Rija and Hassan, 2011
Wildebeest	Ngorongoro Crater, Tanzania	34.6	Talbot and Talbot, 1963
	Ngorongoro Crater, Tanzania	45.2	Estes, 1967
	Hwange NP, Zimbabwe	0.23-1.26	Chamaillé-Jammes et al., 2009
	Continent average	1.87	Pettorelli et al., 2009
	Simanjiro Plains, Tanzania	9.12	Rija and Hassan, 2011
Zebra	Ngorongoro Crater, Tanzania	19.2	Turner and Watson, 1964
	Serengeti NP, Tanzania	9.5	Kruuk, 1972
	Kruger NP, South Africa	0.7-2.2	Smuts, 1975
	Katavi NP, Tanzania	5.64	Caro, 1999
	Lake Mburo NP, Uganda	21.8	Rannestad et al., 2006
	Katavi NP, Tanzania	11.901	Caro, 2008
	Hwange NP, Zimbabwe	0.8-1.92	Chamaillé-Jammes et al., 2009
	Mpala Research Centre, Kenya	1.3	Augustine, 2010
	Simanjiro Plains, Tanzania	19.69	Rija and Hassan, 2011

Table 4. Selected densities used to estimate carrying capacities of nine herbivore species in Manyara Ranch and carrying capacities used in population viability analyses.

Species	Density	Carrying Capacity
Dikdik	13.5	2400
Eland	2.4	440
Elephant	1.74	310
Giraffe	5.3	960
Grant's gazelle	3.31	600
Thomson's gazelle	2.45	450
Impala	11.6	2100
Wildebeest	9.12	1600
Zebra	21.8	3700

A basic population viability analysis (PVA) was run for each species. In each PVA, the average lambda and standard deviation was utilized to model 100 trials of 100 years. Population estimates from the 2014 long rain season were used as initial populations. Population persistence was calculated as the percentage of the trials that were still present after 100 years. I considered a population that persisted in 100 years to be viable, with any populations having over 90% persistence to be of least concern.

I simulated the effects of three different periodicities and three different intensities of drought on population viability for each species. Periodicity simulations included droughts at 5-, 10-, or 20-year intervals for each PVA trial. Intensity simulations included population reductions of either 10%, 20%, or 30% (henceforth referred to as low, medium, and high intensities, respectively) at each simulated drought. These declines were not taken from any specific case study, but were informed by previous research on the impacts of droughts on ungulate populations (Augustine, 2010; Georgiadis et al., 2003; Ogutu and Owen-Smith, 2003).

It should be noted that these periodicities and intensities did not reflect any specific situation but rather examined potential scenarios, some of which may be more likely than others. Furthermore, this study was not looking at droughts of a specific rainfall; instead, it was examining the impacts of drought on species individually due to the fact that certain species handle drought better than others. A real-world drought that results in a 30% decline in one species might not cause the same severity of a decline in another, and thus all species should be examined independently of one another.

Each model of 100 trials was rerun ten times, with the final persistence percentage recorded each time. The ten percentages were then averaged together to provide a persistence percentage estimate. This was done to stabilize the findings, as the random nature of the models meant that the final result of a specific simulation could vary up to 15 percentage points from the next simulation.

These models relied on several assumptions. For the models to have predictive power, I assumed that population estimates were representative of actual populations in MR for both data collected by MR researchers and by SFS researchers. A corollary assumption was that the parameters dictated by these estimates provided accurate population models. Furthermore, I assumed that drought scenarios were indicative of future conditions.

Statistical significance was tested through the use of JMP Pro 11 software (JMP® Version Pro 11, 2013). There were no between-species comparisons, but within each species, a factorial Analysis of Variance (ANOVA) was run with a follow-up Tukey HSD to examine whether differences in persistence percentage were significant and whether

drought periodicity, intensity, or a combination of both was the factor with the greatest impact on persistence. For species with data not normally distributed, data were ranked and then ranks were utilized to run a factorial ANOVA.

Results

Most species had the average population reach an equilibrium near the carrying capacity over the 100 years for the baseline model (Figure 1). Elephants had a rapid decline to extinction within 20 years, but all other species had average populations persist over the 100-year timeframe.

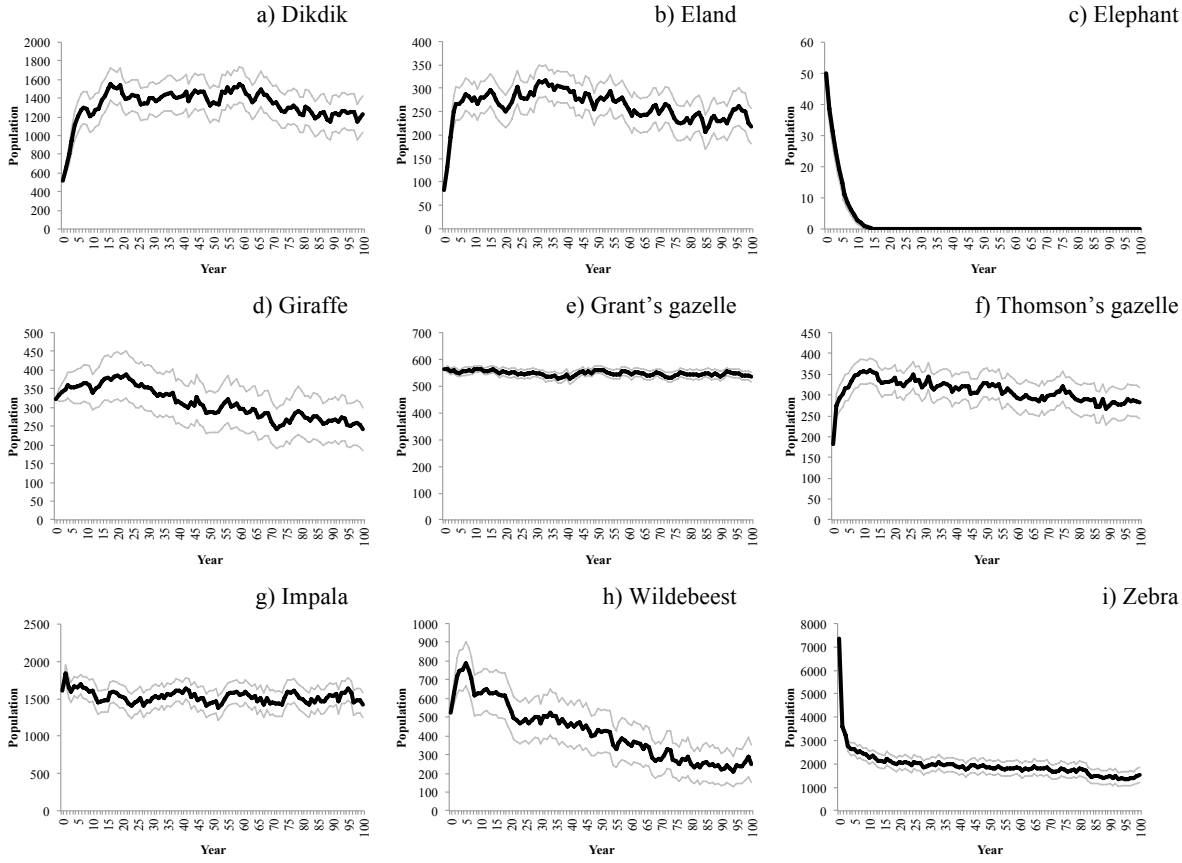

Figure 1. Average projected baseline populations over 100 years for select species in Manyara Ranch, Tanzania, with 95% confidence intervals (gray lines). Each projected population based on a population viability analysis.

Seven species showed a baseline persistence percentage of 70% or higher before the simulation of droughts (Table 5). The exceptions were wildebeest (39.7%) and elephant (0.0%). Elephant populations consistently went extinct within 20 years, regardless of whether droughts were simulated or not. Conversely, Grant's gazelle had a baseline of 100% survival, and only negligible declines in survival percentage seen in the most extreme scenario (high intensity droughts every five years, resulting in a survival percentage of 97.9%) (Figure 2).

Table 5. Percentage of trials demonstrating population persistence over 100 years for baseline (non-drought) PVA models of selected species.

	Persistence %	**Standard deviation**
Dikdik	84.1	5.3
Eland	70.4	4.1
Elephant	0.0	0.0
Giraffe	75.8	4.3
Grant's gazelle	100.0	0.0
Thomson's gazelle	81.2	5.6
Impala	93.1	1.8
Wildebeest	39.7	2.7
Zebra	79.9	4.7

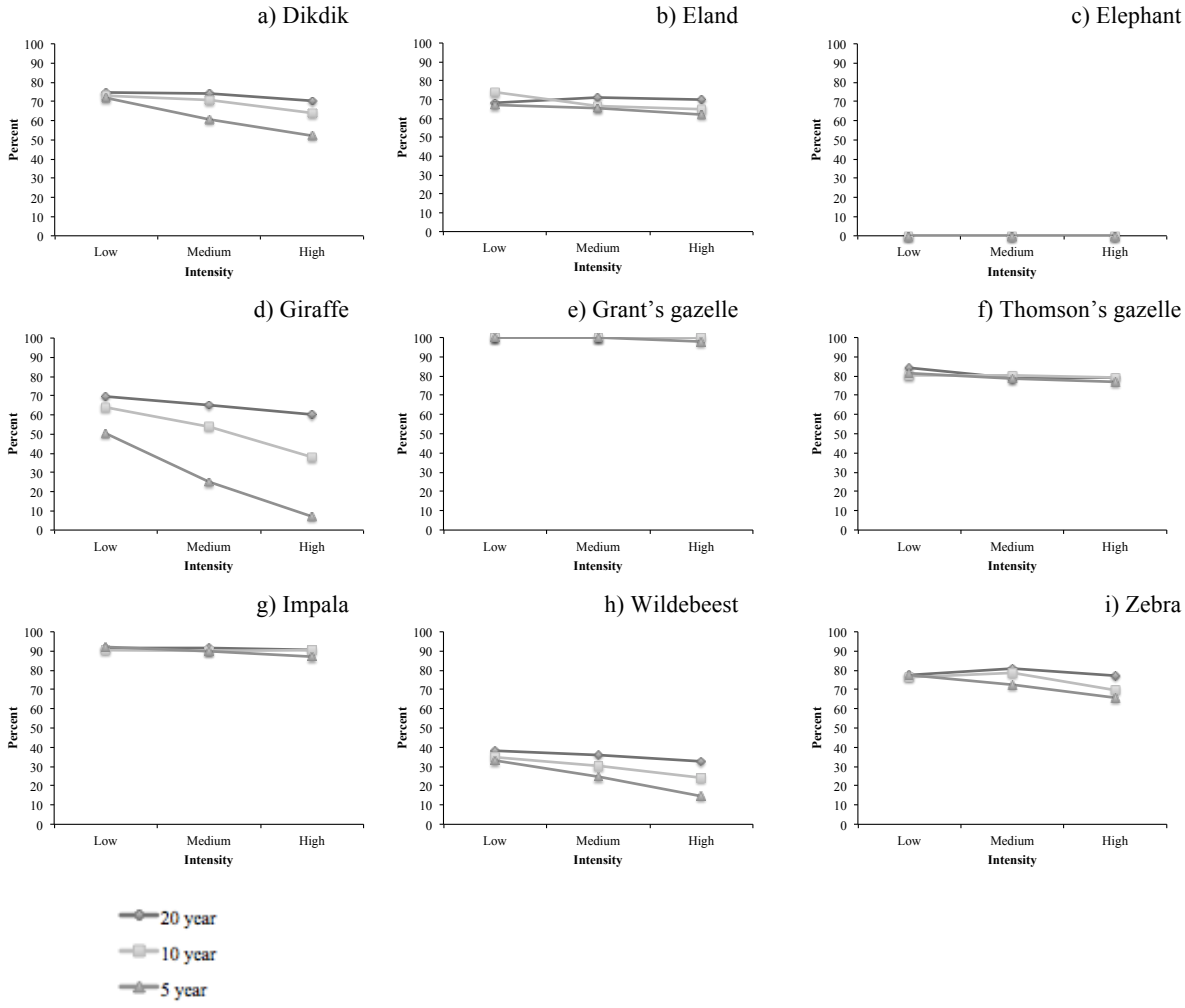

Figure 2. Percentage of trials demonstrating population persistence over 100 years by periodic population drops of varying intensities and periodicities.

All species (with the exception of elephant, which did not provide results allowing statistical analysis) did have significant differences between the results of at least two of the models (Table 6). Thomson's gazelle were the only species that did not have a significant difference between the baseline and any of the sensitivity models (a significant result was found between 20-year, low intensity and 5-year, high intensity), and thus were the only species that did not have a persistence percentage for the 5-year, high intensity model that was significantly different from the baseline. Dikdik and giraffe exhibited significant differences between the baseline and all other models. R^2 values varied from 0.18 for impala to 0.85 for giraffe.

Table 6. Significance of results of population models including periodic droughts of 20-, 10-, and 5-year periodicities and low (10% population reduction; L), medium (20% population reduction; M), and high (30% population reduction; H) intensities. Asterisks indicate results significantly different from baseline persistence percentage. P-value and R^2 are for entire species model.

	20 years			10 years			5 years				
	L	**M**	**H**	**L**	**M**	**H**	**L**	**M**	**H**	**P-value**	**R^2**
Dikdik	*	*	*	*	*	*	*	*	*	<0.0001	0.78
Eland									*	<0.0001	0.32
Elephant										[1]	[1]
Giraffe	*	*	*	*	*	*	*	*	*	<0.0001	0.85
Grant's gazelle									*	<0.0001	0.70
Thomson's gazelle										0.0081	0.21
Impala									*	0.0290	0.18
Wildebeest			*		*	*		*	*	<0.0001	0.63
Zebra						*		*	*	<0.0001	0.56

[1] No statistical analysis run on elephant.

Discussion

Widespread declines in wildlife throughout East Africa are a conservation concern, particularly in the face of likely increased rainfall variably brought on by climate change (Thuiller et al., 2006). In this study, the populations of nine species were projected 100 years into the future, with models of either no droughts (baseline PVA) or with droughts of 20-,10-, or 5-year periodicities and low, medium, or high intensities. In general, the lowest survival percentages were seen for more frequent and intense droughts, with dikdik and giraffe being the most sensitive to any kind of drought. Results suggest that elephants and wildebeest are of highest extinction concern because they experienced the greatest declines in the models, while Grant's gazelle are the least concern.

Conclusions from the baseline model show that elephants are the highest priority species. Due to the open nature of the study area and the fact that relatively dense elephant populations are known in neighboring LMNP and TNP, it should not be definitively assumed that elephants will be extinct in MR within 20 years; however, it does show that they have a pressing need for immediate management action. Furthermore, this conclusion of extinction within two decades is corroborated by the findings of the African Elephant Summit held in Kasane, Botswana, in 2015, which

concluded that if no immediate actions are taken, wild African elephants will be extinct within twenty years (Beaudufe, 2015). Elephant declines are driven heavily by poaching and by habitat loss and fragmentation (Blanc, 2008), which are likely contributing factors in MR as well. These results make it challenging to draw conclusions about the impacts of droughts on elephant populations (although the current situation makes potential droughts irrelevant), but other models have found that deaths from droughts can have a considerable impact on elephant populations (Armbruster and Lande, 1993). If this is the case, then conserving elephants becomes not only an issue of protecting habitat and preventing poaching, but also understanding how to minimize the impacts of droughts on the population.

Following elephants, wildebeest were the second highest priority species in the baseline models and had a persistence percentage considerably lower than the remaining seven species. This is not surprising, considering the extreme declines that wildebeest have experienced in recent years (Stoner et al., 2006; Tanzania Wildlife Research Institute, 2001). Wildebeest are particularly sensitive to loss of habitat to agriculture, which is cited as the major factor in their decline in the Maasai Mara ecosystem; however, rainfall fluctuations and competition with cattle should not be ruled out as influencing factors (Ottichilo et al., 2001). Loss of habitat emphasizes the need for areas like MR in conserving wildlife, although current levels of protection do not appear to be adequate for maintaining wildebeest populations into the future. Management of MR should additionally be aware of the potential impacts cattle may have on wildebeest populations—although whether these impacts are enough to overcome other benefits brought to the ranch by cattle grazing are open for debate—and the exact impacts of cattle presence on wildebeest and other wildlife in MR could be an area of future investigation.

Other species were of moderate extinction concern. Of the three resident species—dikdik, giraffe, and impala—giraffe had the lowest baseline survival percentage, as the species went extinct in approximately one quarter of the trials. In the first decade of the 2000s, giraffe populations continent-wide declined by 40%, with major threats including bush meat poaching and habitat degradation (Dagg, 2014). Local giraffe are thus likely faring better than the continent average, but further monitoring is

warranted. The local subspecies, the Maasai giraffe, is the most populace giraffe race, although they have seen recent declines of up to 60% (Fennessy, 2012). Meanwhile, the other resident species can be considered to have healthier populations, as if a basis of 90% survival is used for a definition of least concern, then impala can be considered a healthy population, while dikdik are only moderately below the threshold. Due to the non-migratory nature of these three species, and thus the fact that most individuals are likely to linger in MR and provide more accurate population estimates, the weight given to the conclusions drawn from these models can be higher than those of the migratory species.

Of the migratory species, Grant's gazelle are a species of least concern in MR, having a viable population predicted for the next 100 years should conditions remain the same. The population projections for zebras may be somewhat misleading, making it appear that the species is worse off than it is, but the sharp initial decline is merely a by-product of the model having a lower carrying capacity than the starting population; overall, zebras demonstrated populations that remained fairly close to the carrying capacity. The extreme variability of zebra populations from year to year makes it more difficult to accurately predict the trajectory, but it appears that while the local zebra population is likely to persist, there is a need for further monitoring and management. Currently, poaching is considered the major threat for zebras in the northern half of their range, while habitat loss is having more of an impact in the south (Hack and Lorenzen, 2008). Eland should be treated with caution, and Thomson's gazelle, while below a 90% viability threshold, appear relatively stable.

Results show that the interaction between drought intensity and periodicity has a greater influence on the projected survival of a species than either factor alone. For dikdik and giraffe, persistence dropped between the baseline and all models, suggesting that these species will be more sensitive to droughts. Giraffe in particular showed considerable responses to increases in drought persistence and intensity, with the lowest survival percentage of all species except elephants in the 5-year, high-intensity model. This is in direct contrast with the physiology of giraffes, which are adapted for arid environments, particularly in terms of their water uptake, which comes mostly from the consumption of vegetation (Dagg, 2014). Dikdiks are similarly adapted for arid

environments, which would suggest limited impacts from droughts; however, dikdiks also are most abundant in areas that have been overgrazed by zebras and wildebeest (Estes, 2014). Thus, their decline could in part be linked to the decline of these species. Conversely, impala, the other non-migratory species, showed negligible changes, with the only significant variation from the baseline being the extreme model of 5-year, high-intensity droughts, and this being significant by only a small margin, suggesting that impala are likely to persist even in the face of increasing droughts. This conclusion is aided by the fact that periodicity and intensity only provide a small amount of the explanation for variations between models for impala. In terms of migratory species, Thomson's gazelle did not have a significant variation from the baseline, suggesting that the one significant result, between 20-year, low-intensity droughts and 5-year, high-intensity droughts, is not particularly meaningful, especially considering the low R^2 value. The significance for Grant's gazelle is unlikely to be meaningful either, despite the R^2 value, as the only variation occurred in the 5-year, high intensity model, but the persistence percentage was still well above the 90% viability threshold. There are few studies on the demographics of Grant's gazelle, making it difficult to determine why this species appears to be faring so well, although they are adaptable to a wide variety of habitats, especially arid environments, which could offer some explanation (Kingdon, 1997). Wildebeest continue to be a priority species in the face of droughts, although only approximately half the models were significantly different from the baseline. Increased concern should only be considered for zebra and eland if droughts become more extreme. Notably, zebras and other large-bodied savannah ungulates tend to have populations that experience greater declines during dry periods than increases during wet periods, which is why droughts can have such devastating impacts on viability (Georgiadis et al., 2003). The general lack of significant differences between the baseline and less frequent and less intense droughts for most species suggests that such stochasticity already exists in the populations and was thus inherently incorporated into the models; in fact, known 18-year cycles of drought match closely with the 20-year models, while shorter cycles of rainfall patterns could likely have been captured in the study period (Mason and Jury, 1997).

The conservation concern of all species should be considered in terms of their ecology, with specific attention to their water-dependency. Of the studied species, dikdik,

eland, giraffe, and Grant's gazelle are water-independent and can survive more easily in more arid conditions than the other five subject species (Estes, 2012). For instance, although zebra and eland have similar survival percentages for the 5-year, high-intensity model, zebra are more susceptible to such a situation where drought causes a 30% drop in total population, as subtler decreases in rainfall will have a more notable impact on the population than they would on eland, and eland would require more drastic decreases in water availability before the same die-offs would be seen. As wildebeest and elephant are both water-dependent species, this only expounds the conclusion that these species are of critical priority. It is also possible that the low baseline survival percentages seen in these species is already an indicator of reactions to decreased water availability, while the high baseline for Grant's gazelle, a water-independent species, is an indicator of its adaptability in the face of water shortages, although more research would be required to make any sort of conclusions.

There are several shortcomings of this study, most notably involving the quality of the data, although data for MR is still better than what can be found in many other neighboring areas. While data were collected periodically from 2003 onward, they were not collected with seasonal regularity until the end of 2011. Missing years had to be filled in as best possible for purposes of creating the models, which while not negating conclusions reached could lend them slightly less power. This emphasizes the importance of continued and regular population monitoring in and around MR, as not only does that allow immediate insights onto population levels, but it also provides potential for reevaluation of projected populations with a stronger dataset. The status of these populations as open and often migratory is another shortcoming, as it led to often more variable lambda values when creating the models. To this end, further studies into more exact carrying capacities for each species specifically within MR could lead to more accurate results; beyond, conducting similar studies in other locations would provide a basis of comparison both in terms of accuracy of results and in terms of conclusions drawn. This study only examined populations in one season (long rains), and it is possible that results for some species could come out differently for different seasons; notably, the wildebeest density in MR during the dry season is on average twice as high as the density during the long rains. Comparing projected survival by season could provide some

valuable insights into the states of these populations, although more data would be required before this could be attempted. Overall, continued monitoring is critical, but more aggressive management tactics should be enacted to conserve species.

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Appendices

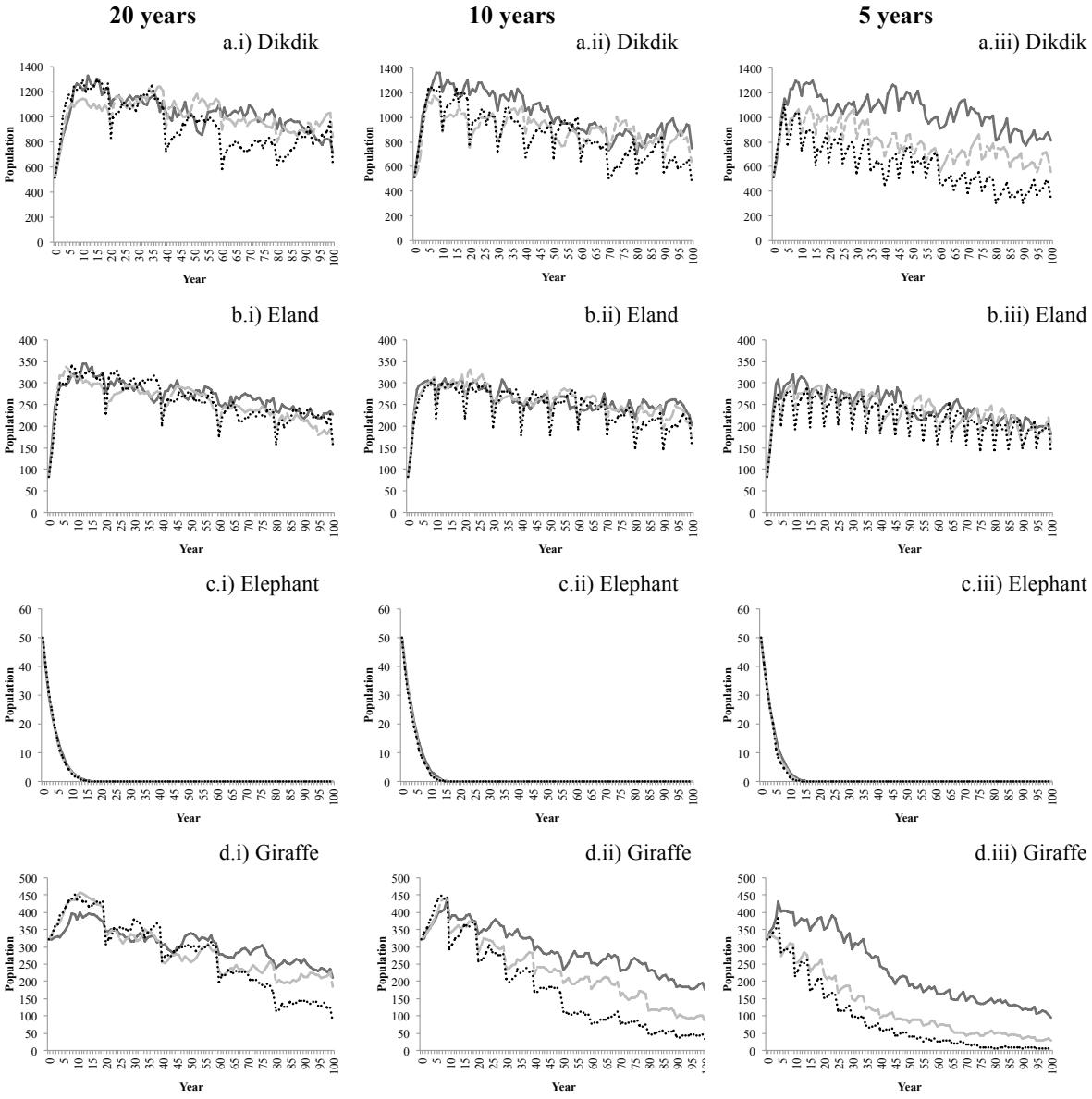
Appendix I

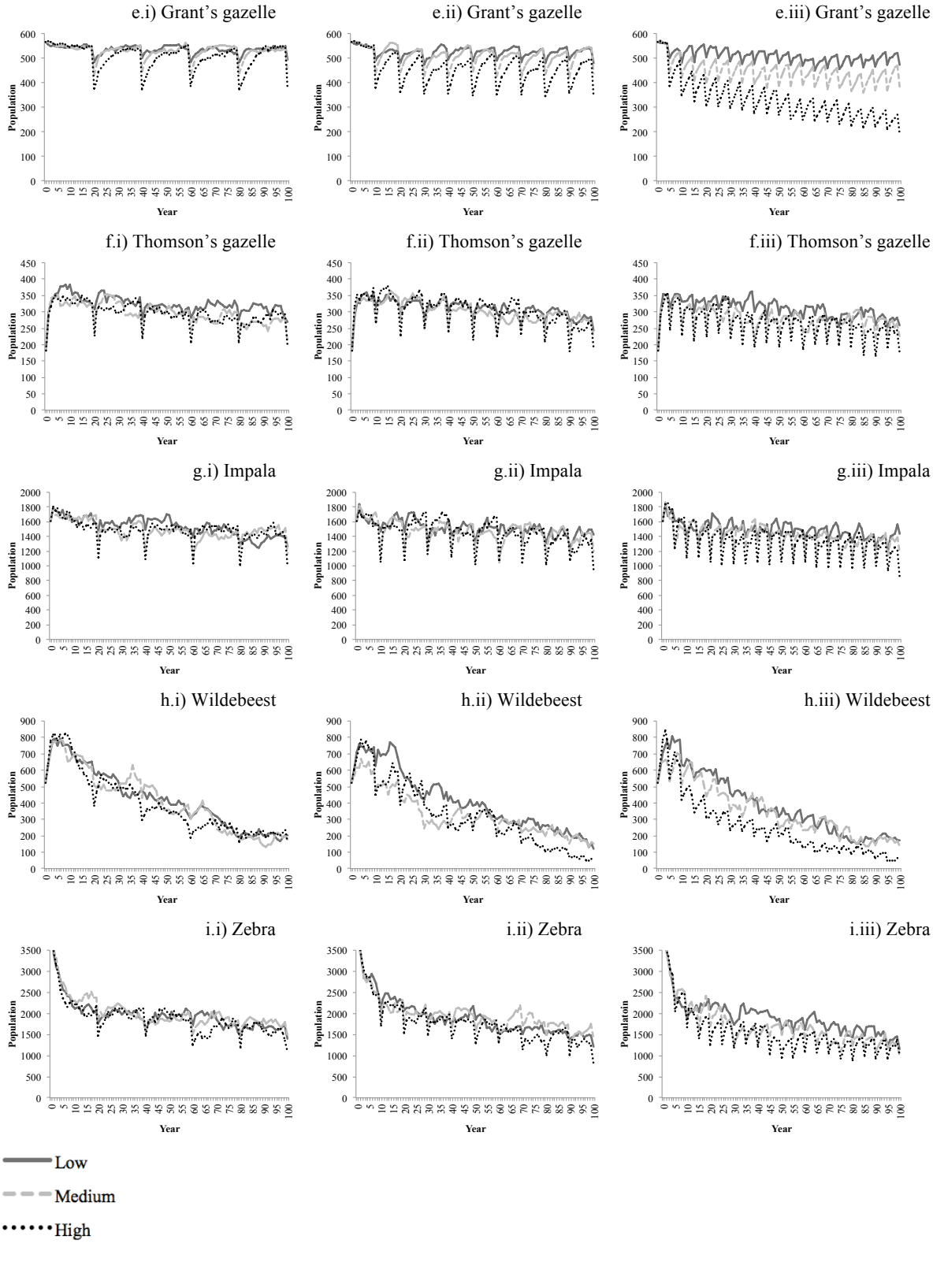
Average lambda (λ), standard deviation of lambda values, and 2014 long rains population estimates used as starting populations, used for parameters of creating species PVA models.

	λ	Standard deviation	Starting population
Dikdik	1.266	0.595	515
Eland	1.442	1.413	82
Elephant	0.802	0.328	50
Giraffe	1.040	0.271	323
Grant's gazelle	1.099	0.181	565
Thomson's gazelle	1.630	1.240	182
Impala	1.463	1.772	1604
Wildebeest	1.154	0.668	526
Zebra	1.319	0.935	7373

Appendix II

Average predicted populations for select species in Manyara Ranch, Tanzania, as dictated by periodic population drops of varying periodicity (20-, 10-, or 5-year increments) and intensity (10%, 20%, or 30% drops in population).




e.i) Grant's gazelle
e.ii) Grant's gazelle
e.iii) Grant's gazelle
f.i) Thomson's gazelle
f.ii) Thomson's gazelle
f.iii) Thomson's gazelle
g.i) Impala
g.ii) Impala
g.iii) Impala
h.i) Wildebeest
h.ii) Wildebeest
h.iii) Wildebeest
i.i) Zebra
i.ii) Zebra
i.iii) Zebra
Population
Year
Low
Medium
High

Appendix III

Average seasonal density (individuals per km^2) and standard error of nine herbivores in Manyara Ranch, Tanzania, from 2003 to 2014. Seasons are long rains (Feb-May), dry (Jun-Oct), and short rains (Nov-Jan).

	Long Rains	**Dry**	**Short Rains**
Dikdik	1.48 ± 0.34	2.17 ± 0.71	3.04 ± 0.50
Eland	1.08 ± 0.58	0.25 ± 0.14	0.22 ± 0.15
Elephant	0.30 ± 0.08	0.61 ± 0.21	0.89 ± 0.51
Giraffe	2.21 ± 0.44	1.74 ± 0.30	1.88 ± 0.45
Grant's gazelle	2.24 ± 0.27	1.23 ± 0.29	1.92 ± 0.58
Thomson's gazelle	0.67 ± 0.24	1.21 ± 0.44	1.19 ± 0.40
Impala	7.62 ± 1.67	7.64 ± 1.46	6.34 ± 1.68
Wildebeest	7.38 ± 3.04	17.05 ± 5.28	6.84 ± 1.99
Zebra	34.46 ± 12.62	29.80 ± 12.20	15.22 ± 4.13

Appendix IV

Statistical results of factorial ANOVAs and Tukey HSD follow-up tests on the persistence percentages of herbivore species in Manyara Ranch, Tanzania. Models with matching letters are not significantly different. All species results are independent of other species. No statistical tests run on elephant results.

Model	Significance	Degrees of Freedom	F Ratio	p-value
Dikdik		99	36.1461	<0.0001
Baseline	A			
20 years, low	B			
20 years, medium	B			
20 years, high	B C			
10 years, low	B			
10 years, medium	B C			
10 years, high	C D			
5 years, low	B			
5 years, medium	D			
5 years, high	E			
Eland		99	4.8094	<0.0001
Baseline	A B			
20 years, low	A B C			
20 years, medium	A B			
20 years, high	A B			
10 years, low	A			
10 years, medium	A B C			
10 years, high	B C			
5 years, low	A B C			
5 years, medium	B C			
5 years, high	C			
Giraffe		99	56.9561	<0.0001
Baseline	A			
20 years, low	B			
20 years, medium	B C			
20 years, high	C D			
10 years, low	B C			
10 years, medium	D E			
10 years, high	E F			
5 years, low	D E			
5 years, medium	F G			
5 years, high	G			
Grant's gazelle		99	23.4852	<0.0001
Baseline	A			
20 years, low	A			
20 years, medium	A			

| | | |

Zebra						99	12.5439	<0.0001
	Baseline	A						
	20 years, low	A	B					
	20 years, medium	A						
	20 years, high	A	B					
	10 years, low	A	B					
	10 years, medium	A	B					
	10 years, high			C	D			
	5 years, low	A	B					
	5 years, medium		B	C				
	5 years, high				D			